

# Effects of some root-grazing arthropods on the growth of sugar-beet

R. A. BROWN

*Broom's Barn Experimental Station, Higham, Bury St Edmunds, Suffolk, IP28 6NP*

## SUMMARY

- 1 The soil-pest complex of sugar-beet comprises a collembolan *Onychiurus armatus* (Tullberg), a symphylan *Scutigerella immaculata* (Newport) and some millipedes, principally *Blaniulus guttulatus* (Boscowan). The establishment and growth of sugar-beet in soils infested with these root-grazing arthropods was studied during 1981.
- 2 The feeding of these arthropods on sugar-beet roots had both lethal and sub-lethal consequences, affecting both plant survival and productivity.
- 3 A typical pattern of spatial and temporal plant survival was found to be associated with this damage.
- 4 At pest-infested sites, yields appeared to be lower than would be expected from the number of plants surviving as a proportion of the number of seeds sown. Though individual plants, damaged but not killed, compensated by growing quickly in the latter half of the season, this was not as much as would be expected from undamaged plants, and was not sufficient to compensate for the yield of all the plants killed by the pests.
- 5 Self-thinning was greater in the plots protected from root grazing by a pesticide.
- 6 Arthropod grazing of the sugar-beet roots increased the abundance, but not the diversity, of weed species competing with the crop; it also decreased the dominance of sugar-beet, defined as the ratio of the population density of sugar-beet to the total population density of all plant species found.

## INTRODUCTION

Sugar-beet was derived from the common coastal plant, sea beet *Beta vulgaris* ssp. *maritima* L., and is now cultivated all over the world. In England and Wales, sugar-beet seedlings are attacked by a collection of arthropods known as the 'soil-pest complex' (Brown 1981), comprising a symphylan, *Scutigerella immaculata* Newport, the millipedes *Blaniulus guttulatus* (Boscowan), *Boreoiulus tenuis* (Bilger), *Archeboroiulus pallidus* (Brade-Birks) and *Bracydesmus superus* (Latzel), and a collembolan, *Onychiurus armatus* (Tullberg) (*s. l.*). These animals damage sugar-beet by feeding on the roots of the seedlings; the plants appear to become

Present address: Department of Pure and Applied Biology, Imperial College, Silwood Park, Ascot, Berkshire. SL5 7PY.

resistant to this damage by the time they have developed four true leaves (Jones & Dunning 1972). Though the plants are injured by the direct effects of feeding, there are often invasions of fungal pathogens (and occasionally nematodes) following damage, which could also contribute to the observed mortality.

The animals of this complex pass their whole life cycle in the soil and rarely come above the surface. The symphylan, *S. immaculata*, overwinters deep in the soil (Edwards 1959) and comes near to the surface to feed in late April in East Anglia (early to mid-May in Yorkshire), disappearing from the surface layers of the soil by mid-June. *S. immaculata* reappears at the surface during September. The millipedes and collembolan do not migrate vertically in the soil to the same extent as *S. immaculata* and can usually be found, all year round, in the top 15 cm of agricultural fields.

Decreases in plant productivity have been found when Collembola are allowed to feed on mycorrhizas of leek plants (Warnock, Fitter & Usher 1982; Finlay, p. 319), without feeding on the actual plant roots themselves. Sugar-beet is not known to support a mycorrhiza (Harley 1969), but is often associated with fungal pathogens. Many species of fungi may be involved, including *Aphanomyces*, *Fusarium*, *Phoma*, *Pythium*, and occasionally *Rhizoctonia*. Ulber (1983) has shown that, in Germany, the feeding of *Onychiurus fimatus* Gisin on *Pythium ultimum* Trow., parasitic on the roots of sugar-beet plants, can decrease the infestation of the fungus and increase the probability of plant survival.

## MATERIALS AND METHODS

### *Ramsey Forty Foot*

At Ramsey Forty Foot, Cambridgeshire, where the soil was a silty peat, 8 plots (30 × 12 m) were sown on 26 March 1981. The sugar-beet seed (cv. Nomo) was spaced at 20 cm, in rows 50 cm apart. Carbofuran granules (Bayer UK Ltd.) were applied in the seed furrow at a rate of 600 g active ingredient ha<sup>-1</sup> to four of the plots, whilst four others were untreated. Carbofuran is effective against root-feeding arthropods (and nematodes) but is not particularly systemic, so its activity is confined to root feeders. All the plots were treated with the pre-emergence herbicide mixture of protham, chlorprotham and fenuron and a post-emergence treatment of phenmedipham, at manufacturers' recommended rates.

Destructive growth analysis was performed on five occasions from June to September, and a final harvest was made on 16 October. For the destructive growth analyses, ten plants were taken from each plot according to a predetermined random sequence, taken to the laboratory, and divided into roots and shoots (leaves + petioles). The root and shoot fresh weight from each plot was recorded, and weighed subsamples were then dried to a constant weight at 85°C. At final harvest, roots from 10 m of row, from the centre three rows of each plot, were lifted, topped and destructively analysed.

During the cotyledon stage of growth, three soil cores (5 cm in diameter and 15 cm deep) were taken from each treated plot, and three from each of the untreated plots. The animals in the cores were expelled from the soil in a Rothamsted type controlled gradient extractor (Brown 1982), collected in a 9:1 mixture of 70% ethanol and glycerol, and counted. In August, the species and population densities of weeds in the plots were recorded.

#### NORTH NEWBALD

At North Newbald, Humberside, the crop (cv. Bush Mono G) was drilled on 21 April 1981 at a spacing of 9.5 cm. The soil was a calcareous very fine sandy loam. The plots (15 × 5 m), part of a larger experiment, were in four blocks, in each block there was an untreated plot and one treated with carbofuran, as at Ramsey Forty Foot. On 11 June the interplant distances between approximately 125 plants from the middle three rows of each plot were measured on each of the four experimental blocks. Soil cores were taken, as at Ramsey Forty Foot, from the treated and from the untreated plots when the plants were in the cotyledon stage, and the numbers of animals caught were assessed.

### RESULTS AND DISCUSSION

#### *Effects on the animals*

Table 1 shows that at both sites the pesticide decreased the abundance of the soil-pest complex in the plots. Significant decreases were noted for *O. armatus* at Ramsey Forty Foot and for *S. immaculata* at North Newbald. Both sites were sampled for plant-parasitic nematodes, but very few were found.

TABLE 1. The population densities (animals 1<sup>-1</sup> of topsoil) of the soil-pest complex at Ramsey Forty Foot and North Newbald, May, 1981. Mean densities ± SE are given

|                        | <i>O. armatus</i> | <i>B. gutulattus</i> | <i>S. immaculata</i> |
|------------------------|-------------------|----------------------|----------------------|
| Ramsey Forty Foot      |                   |                      |                      |
| Untreated              | 13.26 ± 5.01      | 4.74 ± 2.17          | 0.85 ± 1.23          |
| Treated                | 4.73 ± 2.61       | 1.87 ± 1.27          | 0.00 ± 0.00          |
| <i>t</i> <sub>11</sub> | 3.21              | 1.82                 | —                    |
| Probability            | < 0.01            | ns                   | —                    |
| North Newbald          |                   |                      |                      |
| Untreated              | 12.24 ± 8.91      | 0.55 ± 0.85          | 10.57 ± 4.15         |
| Treated                | 3.45 ± 2.61       | 0.00 ± 0.00          | 3.43 ± 1.52          |
| <i>t</i> <sub>11</sub> | 1.39              | —                    | 2.32                 |
| Probability            | ns                | —                    | < 0.05               |

*Effects on the plants**Lethal effects*

Figure 1 shows the survival of sugar-beet, not protected by a pesticide, grown in a field heavily infested with the soil-pest complex. Here, plants died at a decreasing rate over the first 30 days after emergence as they grew through the cotyledon stage; then there was a drop in the number of plants surviving. As the surviving plants developed beyond this stage and grew two, four and then six true leaves, they became tolerant of the damage and the numbers of plants reached an asymptote at between 60 and 65% of the seeds sown. All the dead plants examined had extensive damage to their root systems. This pattern of plant survival was typical of eleven other sites studied during spring 1981.

The survival of sugar-beet plants in plots protected from the soil-pest complex by carbofuran is shown in Fig. 2. Like the untreated beet, the treated ones die at a

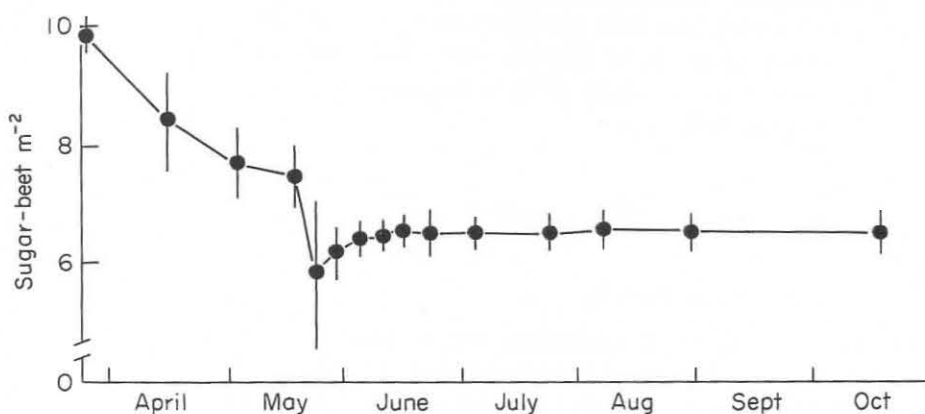


FIG. 1. The temporal pattern of sugar-beet failures in plots unprotected by pesticide at Ramsey Forty Foot, 1981. Mean population densities  $\pm$ SE are shown.

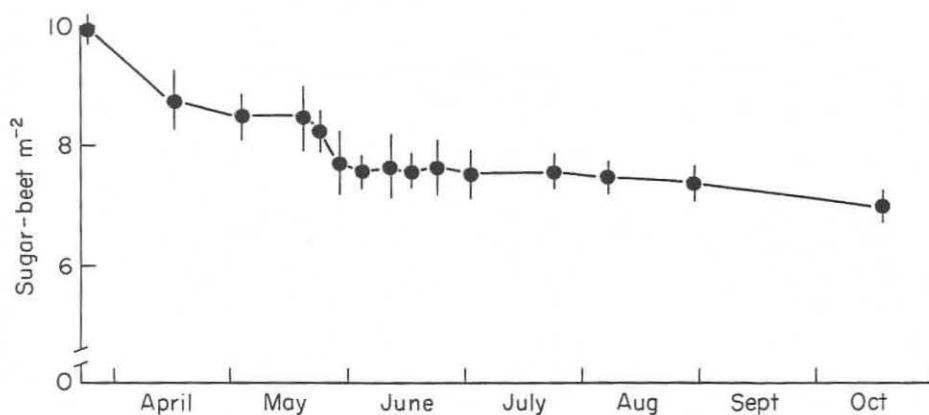


FIG. 2. The temporal pattern of sugar-beet failures in plots protected from the soil-pest complex by the pesticide carbofuran at Ramsey Forty Foot, 1981. Mean population densities  $\pm$ SE are shown.

decreasing rate over the 30 days after emergence, followed by a small drop in numbers during the two true leaf stage. The population density of sugar-beet plants appears to stabilize at about 50–60 days after emergence, there then seems to be a slight decrease again just before harvest.

There is a spatial pattern of plant survival, as well as the temporal one described above, that typifies a sugar-beet crop damaged by the soil pest complex (Fig. 3). Jaggard (1979) found, through surveys and through experiments with crops undamaged by the soil-pest complex, that plant failures occur at random. Brown (1981) found this to be the case at two sites infested with the soil-pest complex, where an effective pesticide was used. Here the number of consecutive seed sta-

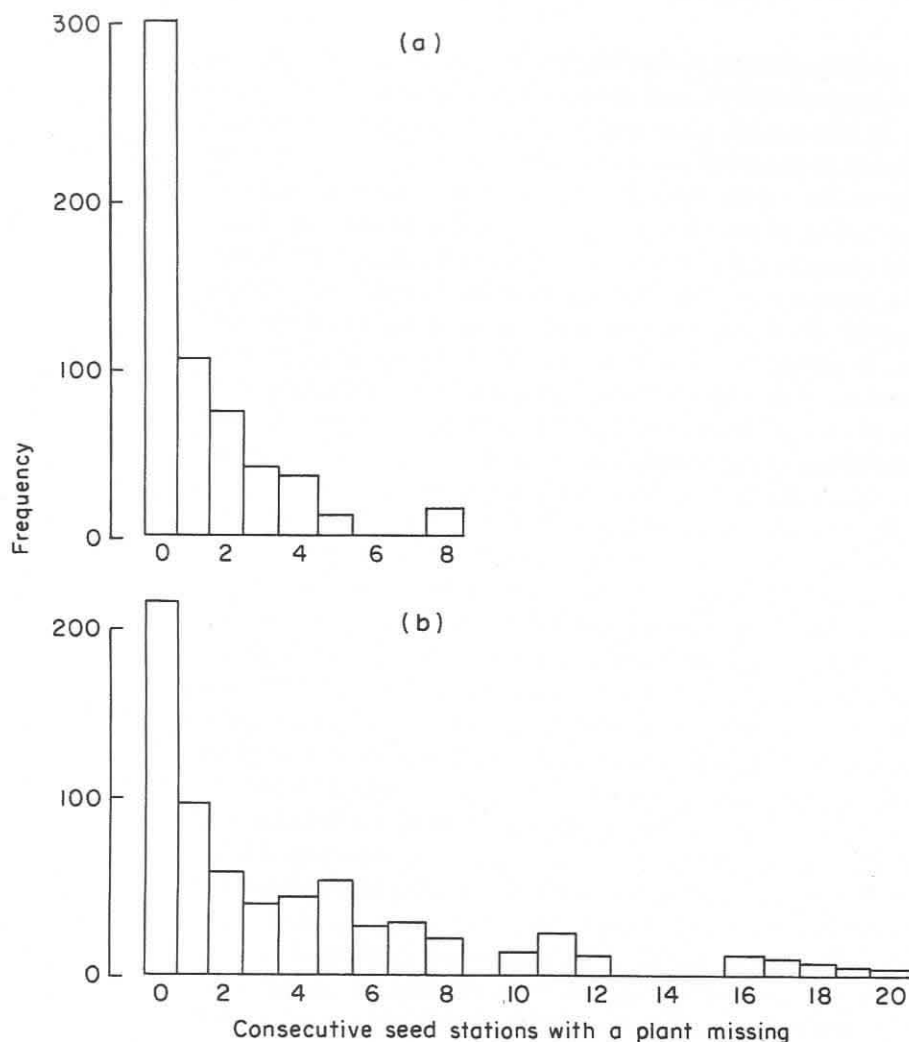


FIG. 3. The spatial pattern of sugar-beet seedling failures at North Newbald, 1981; (a) treated with carbofuran, (b) untreated.

tions that failed could be modelled using the geometric series. Where the soil-pest complex was allowed to aggregate and to feed in the rows of sugar-beet, either through the lack of an effective pesticide or through no treatment, the occurrence of plant failures was contagious and could be modelled using the negative binomial distribution. Hence, in the absence of feeding by the soil-pest complex, and by some vertebrate pests such as the wood mouse *Apodemus sylvaticus* L. (Green 1978), the probability of seedling survival is independent of success or failures at neighbouring seed stations, but this is not the case when the soil-pest complex is active.

#### *Sublethal effects*

A model of sugar-beet yield in relation to seedling establishment and plant spacing has been developed by Jaggard (1979), and verified in the absence of damage by the soil-pest complex. In this model, plant spacings are predicted from the multinomial theorem and yield is predicted from this, using Bleasdale's (1966) yield/plant density equation. If the yields from soil-pest complex infested fields are decreased only through killing plants, then it would be expected that the predictions of Jaggard's model would fit data from such sites; if the model did not fit, then soil-pest complex damage must affect yield through processes in addition to the loss of plants. A suitable, unpublished, data set against which the model could be tested was collected by R. A. Dunning, G. H. Winder and W. A. Thornhill of Broom's Barn Experimental Station, from four sites where they conducted experiments on the efficacy of various pesticides against soil-inhabiting pests. At these sites they measured seedling establishment percentage (the number of plants surviving per 100 seeds sown) and sugar yield at final harvest from a range of treatments. As these pests were the only recorded cause of loss at the sites, it is assumed that the differences in yield from the plots are due largely to different amounts of pest damage caused by the differing effects of the pesticides on the pests.

When the actual sugar yields are plotted against those predicted from the seedling establishment data of Dunning *et al.* (unpubl.) using Jaggard's model (Brown 1982; Jepson & Green 1983), it can be seen that actual sugar yields are lower than the predictions (Fig. 4). Though this discrepancy could be due to differences in soil fertility between these sites and the one at which the model was derived, or due to gaps in the pest-damaged crops in excess of those originally studied by Jaggard, Jepson & Green suggest that it is more likely to be due to the plants being stunted by pest feeding. Whatever the cause, it appears that yield, on a unit area basis, is being lost in excess of that expected from the observed seedling establishment, in those fields where the soil-pest complex is active; this suggests that the productivity of the plants damaged, but not actually killed, by pest attack is lowered.

The accumulation of mean root dry weight  $\text{m}^{-2}$  on the treated and untreated plots is shown in Fig. 5. These data, and data for mean dry weight per plant, were tested using a factorial ANOVA in which the factors were individual sampling occasions and treatment with the pesticide; the mean root dry weights on individual

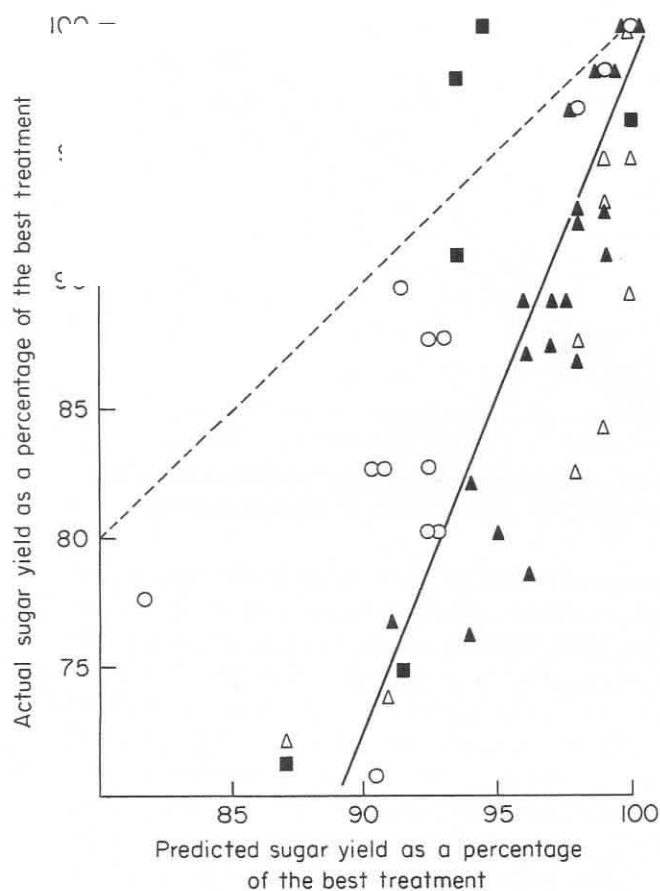


FIG. 4. The relationship between actual sugar yields from plants damaged by soil-inhabiting pests and the yield predicted from Jaggard's (1979) model. The dotted line is the equality line (actual = predicted), and the solid line the best fit to the unpublished data gathered from four different sites (indicated by the different symbols) and kindly provided by R. A. Dunning, G. H. Winder & W. A. Thornhill.

sampling occasions could then compare as linear contrasts (Sokal & Rohlf 1969). At the third harvest, on 22 July, the mean root dry weight per plant in untreated plots was significantly depressed compared to that of the treated ones ( $F_{1,36} = 9.97$ ,  $P < 0.01$ ), but by the final harvest, it was not significantly different from that of the treated plants ( $F_{1,36} = 0.85$ ). The plant roots on the untreated plots were smaller than those in the treated plots early in the year, just after damage by the soil-pest complex had been done, but must have compensated for this by growing more quickly later in the season to a similar final size as the treated plants. The untreated root dry weight  $m^{-2}$  was found to be significantly depressed early in the season ( $F_{1,36} = 11.56$ ,  $P < 0.01$  at the third harvest) and at final harvest ( $F_{1,36} = 16.57$ ,  $P < 0.001$ ), largely as a consequence of the lower plant population density.

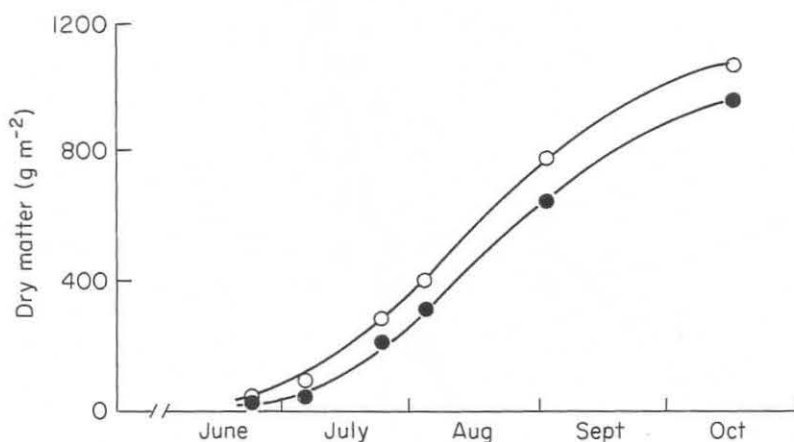


FIG. 5. The accumulation of dry matter in the roots of sugar-beet protected from the soil-pest complex by the pesticide carbofuran (○) and unprotected (●). The dry matter per unit area is shown.

It appears that individual sugar-beet plants can compensate for damage to their roots through an increased growth rate in the latter half of the growing season; this is perhaps due to reduced competition between plants because of lower plant populations where there has been damage by the soil-pest complex. This compensation, however, is less than would be expected. Individual roots from the untreated plots were of a similar dry weight to the treated ones at final harvest, we would expect them to be larger as they were growing in a less dense plant population (Figs 1 and 2). This discrepancy is consistent with the hypothesis that the productivity of damaged plants is lowered, the final yield of individual pest-damaged plants being less than would be expected; it is not possible to say whether this is due to excessive gappiness or to reduced root efficiency. Though individual plants compensated, to an extent, for damage done at an early stage by the soil-pest complex, this was not sufficient to replace the yield of the plants that died as a result of pest damage; this resulted in the yield per square metre remaining significantly less in the untreated plots throughout the season.

## CONSEQUENCE OF THIS DAMAGE

### *For plant competition*

#### *Intraspecific competition*

The plants at Ramsey Forty Foot suffered much higher mortality from soil-inhabiting herbivores (and possibly pathogens) at the seedling stage on the untreated rather than on the treated plots. No further mortality occurred on the untreated plots after the plants had reached the four true-leaf stage. A small but significant ( $t_4 = 3.45$ ,  $P < 0.05$ ) mortality was recorded on the treated plots towards the end of the season.

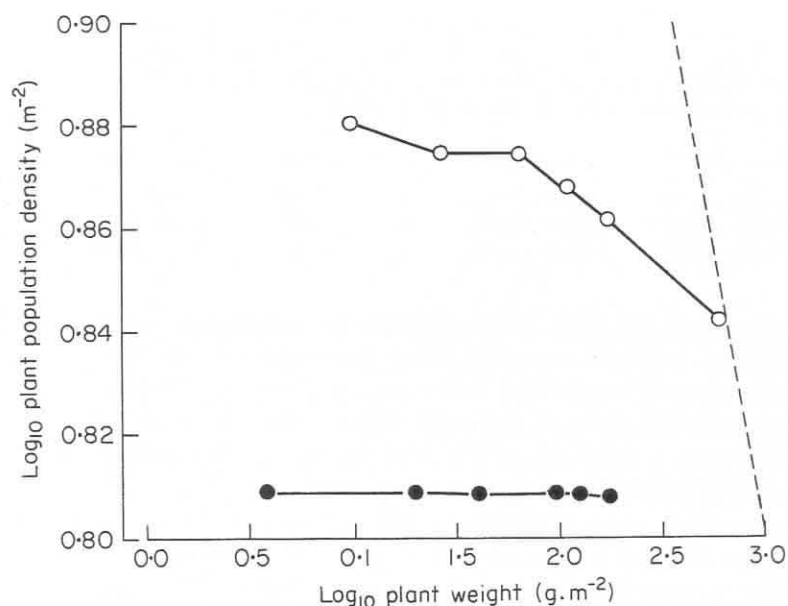


FIG. 6. Self-thinning of sugar-beet at Ramsey Forty Foot. The trajectory in treated plots (○) and in untreated ones (●) is shown. The dotted line is the self thinning line of plant population density against plant weight per unit area, with the predicted slope of  $-2$ .

It is likely that these deaths are due to self-thinning in the crop: the deaths of apparently established plants, most often in the smallest size classes (Harper & White 1974), due to intraspecific competitions. This phenomenon was first quantified by Yoda *et al.* (1963), and their prediction that the ratio of the logarithm of mean plant weight to the logarithm of surviving plant density is  $-3/2$  became known as Yoda's rule. Figure 6 shows the self-thinning effect in the treated plots (open circles) between June and October. Here, the logarithm of surviving plant density is plotted against the logarithm of mean plant weight per unit area, so the (dotted) self-thinning line should have a slope of  $-2$  rather than  $-3/2$  (Crawley 1983). What little self-thinning was noticed occurred in the treated, rather than the untreated plots; in this instance root grazing by the herbivores decreased the number of plant deaths by relaxing intraspecific competition. Before these deaths occurred, the sugar-beet in the treated plots were not at a population density where this would be expected ( $7.2$ , SE  $0.3$  m<sup>-2</sup>). It is possible that the low numbers of contagiously distributed herbivores in the treated plots could make the plants differentially competitive, without severely lowering the surviving plant population density, therefore accentuating self-thinning.

#### *Interspecific competition*

Table 2 shows that though weed diversity was not significantly affected by the different amounts of grazing on the treated and untreated plots, weeds were signifi-

TABLE 2. The effects of grazing by the soil-pest complex on the number of weed species, weed abundance and sugar-beet 'dominance' at Ramsey Forty Foot, Cambridgeshire, August 1981. Weed abundance is expressed as weed plants  $m^{-2}$  and sugar-beet 'dominance' as the ratio of sugar-beet population density to total plant population density. Means  $\pm$  SE are given

|                        | Treated          | Untreated        | <i>n</i> | <i>F</i> ratio | Significance |
|------------------------|------------------|------------------|----------|----------------|--------------|
| Number of species      | 6.75 $\pm$ 0.48  | 7.00 $\pm$ 0.41  | 8        | 0.16           | NS           |
| Weed abundance         | 10.00 $\pm$ 1.47 | 23.25 $\pm$ 4.82 | 8        | 6.91           | $P < 0.05$   |
| Sugar-beet 'dominance' | 0.42 $\pm$ 0.08  | 0.28 $\pm$ 0.09  | 8        | 46.81          | $P < 0.001$  |

cantly more abundant on the untreated plots. It appeared that the larger gaps in the untreated plots, caused by the soil-pest complex killing seedlings, allowed the establishment of a greater number of weeds later in the season. When the soil-pest complex were allowed to graze the roots of the sugar-beet, greater numbers of weeds were able to establish both in and between the rows than where root-grazing was limited by the use of a pesticide. Sugar-beet is often more attractive to the soil-pest complex than many common weeds (Brown 1982). It is possible that there was no effect on weed species diversity because the soil-pest complex do not distinguish between the different weed species at this site or that all the weeds found were equally well represented in the seed bank in this particular field. The dominance of sugar-beet at this site, defined as the ratio of the sugar-beet population density to the total plant population density, is decreased by the feeding of the soil-pest complex.

#### ACKNOWLEDGMENTS

I would like to thank M. J. Crawley, R. A. Dunning, M. J. Durrant, R. E. Green, K. W. Jaggard and G. H. Winder for discussion; J. M. Cooper and J. M. Wardman for assistance, and the farmers, Mr Oswald Rose and Mr Walter Turton. This work was financed in part by the Ministry of Agriculture's Sugar-Beet Research and Education Committee, and by grants from FMC Corporation (UK) Ltd, Union Carbide UK Ltd, Cyanamid of Great Britain Ltd., Rhom and Haas (UK) Ltd, Bayer UK Ltd, Ciba Geigy Agrochemicals, Sandoz Products Ltd, Eli Lilly International Corporation, Hoechst UK Ltd, Pan Britanica Industries Ltd, Murphy Chemicals Ltd and BASF UK Ltd.

#### REFERENCES

- Bleasdale, J.K.A. (1966). The effect of plant spacing on the yield of bulb onions (*Allium cepa* L.) grown from seed. *Journal of Horticultural Science*, **41**, 145–153.
- Brown, R.A. (1981). Gappiness, sugar-beet yield loss and soil-inhabiting pests. *Proceedings of the 11th British Insecticide and Fungicide Conference*, **3**, 803–810.
- Brown, R.A. (1982). *The ecology of soil-inhabiting pests of sugar-beet, with special reference to Onychiurus armatus*. Ph.D. Thesis, University of Newcastle-upon-Tyne.
- Crawley, M.J. (1983). *Herbivory: the Dynamics of Animal-Plant Interactions*. Blackwell Scientific Publications, Oxford.

- Edwards, C.A. (1959). The ecology of the Symphyla, II. Seasonal soil migrations. *Entomologia Experimentalis et Applicata*, **2**, 257–267.
- Green, R.E. (1978). *The ecology of bird and mammal pests of sugar beet*. Ph.D. Thesis, University of Cambridge.
- Harley, J.L. (1969). *The Biology of Mycorrhiza*. Leonard Hill, London.
- Harper, J.L. & White, J. (1974). The demography of plants. *Annual Review of Ecology and Systematics*, **5**, 419–463.
- Jaggard, K.W. (1979). *The effect of plant distribution on the yield of sugar beet*. Ph.D. Thesis, University of Nottingham.
- Jepson, P.C. & Green, R.E. (1983). Prospects for improving the control of sugar-beet pests in England. *Advances in Applied Biology* **7**, 175–250.
- Jones, F.G.W. & Dunning, R.A. (1972). *Sugar Beet Pests*. MAFF Bulletin 162, HMSO, London.
- Sokal, R.R. & Rohlf, F.J. (1969). *Biometry. The Principles and Practice of Statistics in Biological Research*. Freeman & Co. San Francisco.
- Ulber, B. (1983). Einfluss von *Onychiurus fimatus* Gisin Collembola, Onychiuridae) und *Folsomia fimetaria* (L.) auf *Pythium ultimum* Trow., einen Erreger des Würzelbrandes der Zuckerrübe. *New Trends in Soil Biology* (Ed. by Ph. Lebrun, H.M. Andre, A. de Mets, C. Gregoire-Wibo & G. Wauthy), pp. 261–268. Proceedings VIII International Colloquium of Soil Zoology, 1982. Dieu-Brichart, Louvain-la-Neuve, Belgium.
- Warnock, A.J., Fitter, A.H. & Usher, M.B. (1982). The influence of a springtail *Folsomia candida* (Insecta, Collembola) on the mycorrhizal associations of leek *Allium porrum* on the vesicular-arbuscular endophyte *Glomus fasciculatum*. *New Phytologist*, **90**, 285–292.
- Yoda, K., Kira, T., Ogawa, H. & Hozumi, K. (1963). Self thinning in overcrowded pure stands under cultivated and natural conditions. *Journal of Biology of Osaka City University*, **14**, 107–129.